

THE SWIMBLADDER IN AFRICAN
NOTOPTERIDAE (PISCES) AND ITS BEARING
ON THE TAXONOMY OF THE FAMILY

BY

P. H. GREENWOOD

Department of Zoology, British Museum (Natural History)



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INTRODUCTION

THE swimbladder in Asian Notopteridae has long been the subject of discussion and investigation (Cuvier and Valenciennes, 1848 ; Bridge, 1900 ; de Beaufort, 1909 ; Dehadrai, 1957 & 1962 ; Marshall, 1962) but the African representatives (*Notopterus afer* and *Xenomystus nigri*) have never been studied ; authors have tacitly assumed uniformity in this organ throughout the family. Marshall (1962) has recently suggested the importance of swimbladder studies in understanding the higher classification of isospondylous fishes. He also drew attention to the still unsettled taxonomic position of the North American Hiodontidae in relation to the Notopteridae.

In this paper I have attempted both to fill the gap in our knowledge of notopterid swimbladders and to review the phyletic position of the Hiodontidae. A preliminary note on the first aspect of this problem has already appeared (Greenwood,

1963). From the investigations it is clear that the African notopterids differ significantly from their Asian congeners and that these differences must affect the current taxonomy of the family. So, in addition to the anatomical descriptions a short taxonomic section is appended, together with a discussion on the broader taxonomic implications arising from these investigations.

THE SWIMBLADDER OF *NOTOPTERUS AFER**

(i) *Abdominal Part* (Plates 1-4 and Text-fig. 1)

As in the Asian species, the swimbladder is divisible into a cranial (precoelomic), an abdominal and a caudal (post-coelomic) part.

Two subdivisions of the *abdominal* part are easily recognized from external features; there is an anterior, subspherical portion with thick, fibrous and silver-grey walls from which is derived a wedge-shaped posterior projection (most easily discerned on the left side) overlying the second division, a thin walled, muscle

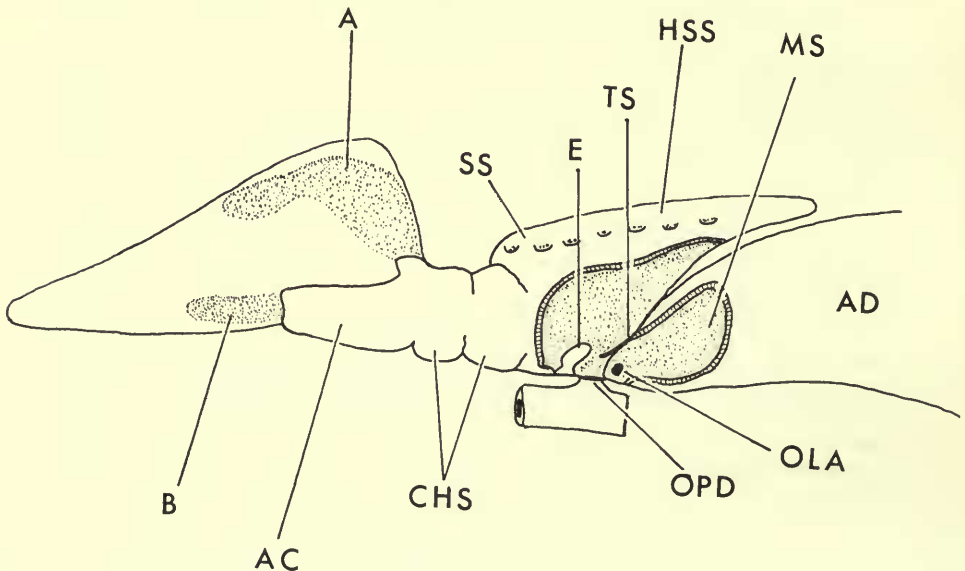


FIG. 1. *Notopterus afer*. Diagrammatic representation of the cephalic and abdominal portions of the swimbladder; left lateral view. Part of the lateral wall is removed from the subspherical sac and the anterior portion of the abdominal section. The crescentic markings on the subspherical sac and its posterior horn represent the points through which the ribs emerge. The neurocranium is indicated diagrammatically in outline. A: superior intracranial diverticulum; AC: auditory chamber; AD: abdominal division of swimbladder; B: inferior intracranial diverticulum; CHS: contiguous hemispheres; E: epiglottis; HSS: posterior horn of subspherical sac; MS: median septum dividing anterior (fused) portion of abdominal swimbladder; OLA: opening to left-hand division of abdominal swimbladder; OPD: opening of pneumatic duct; SS: subspherical sac; TS: oblique transverse septum dividing abdominal and subspherical divisions of the swimbladder.

*Later, this species is placed in a new genus, but throughout the anatomical section it will be referred to by its better known name.

invested, elongate sac (Plates 1 & 2 ; Text-fig. 1). These superficial divisions coincide with internal structural differences which are described below. The large pneumatic duct enters the swimbladder through the base of the subspherical sac near its posterior limits. On first dissection, the division between the subspherical sac and the posterior sac is obscured by a large, descending lobe of kidney. At about the ventral margin of the swimbladder, this kidney lobe sends back a thinner, horizontal lobe which is closely applied to the ventral wall of the bladder over its entire abdominal extent.

The subspherical sac is large, and from it is developed the wedge-shaped projection noted above (Text-fig. 1). Internally, the wedge is divided medially by the vertebral column. Each horn so formed must be considered as a separate diverticulum. The external tunic of the subspherical sac and its horns is very tough and fibrous, having the appearance and feel of leather. Dorsally it is inserted onto the dorsolateral surface of the vertebral column, just above the ribs. The proximal parts of the first seven ribs are thus covered by the *tunica externa*. At the point where each rib curves ventrad it penetrates the tunic and thus comes to lie outside the bladder, closely embracing its lateral wall. The proximal sixth of each rib, after it has left the bladder, is encased in a gutter-like sleeve of *tunica externa* which leaves the dorsal aspect of the rib uncovered ; laterally and ventrally, the tunic sleeve is closely applied to the rib. Within the bladder, each rib is closely covered on its anterior, ventral and posterior face by the thin *tunica interna*.

The subspherical sac is connected to the cranial chamber by means of two, shorter, contiguous, somewhat flattened hemispherical sacs lying above the posterior part of the branchial chamber (Text-fig. 1). The more posterior of these sacs is linked to the subspherical sac through an elongate "waist", lying between the cleithra. Like the abdominally situated subspherical sac, these anterior chambers have a thick, fibrous external tunic. Although not strictly cranial in position, this portion of the bladder will be described with the cranial section.

Internally, the anterior limit of the subspherical sac is recognizable by a low ridge, developed from the *tunica externa*, and appearing as two half rings rising vertically from a median ridge in the floor of the sac (Plate 3). Each half ring runs vertically up the wall of the sac and ends at the vertebral column. A number of similar rings strengthen the walls of the posterior horns arising from the sac. Since the *tunica externa* ends at its insertion on the vertebral column, the roof of the subspherical sac, and the median walls of the two horns, are formed entirely from the very thin *tunica interna*. In preserved specimens this tunic is transparent and since it is intimately applied to the vertebrae, the details of these bones are easily seen (Plate 4).

Anteriorly the lumen of the subspherical sac is continuous with that of the inter-connecting and cranial chambers. Posteriorly, however, it is sealed off from the thin-walled abdominal sac by an almost complete, gently curved and oblique transverse wall. The only perforation in this wall is situated ventrally (see below, p. 382 and Plate 3).

Besides forming a transverse partition, the wall also forms the floor to the

posterior horns of the subspherical sac. It will be recalled that these horns are actually a single, wedge-shaped chamber arising from the subspherical sac and overlie the anterior part of the thin-walled sac ; internally the chamber is divided into two by the vertebral column. The relationship of the horns with the underlying chamber of the abdominal bladder differs in the large and smaller specimens examined. In the two large specimens (48.0 & 53.5 cm. S.L., both females), the wall forms a common boundary between the right horn and the right hand side of the abdominal sac (which is divided into left and right chambers anteriorly by a median vertical septum, see below) ; in the smallest fish (30 cm. S.L. ; possibly a male) there is a common boundary between the horn and the sac on both sides. By contrast, in the large fishes, the left horn is distinct from the underlying abdominal sac, so the continuation of the oblique transverse wall merely forms a floor to the horn (see Plate 3), the sac having its own dorsal wall. Where there is a common boundary between horn and sac (right side in large fishes, both sides in the smaller individual) it is perforated and the two cavities are in communication ; also in these cases, the *tunica externa* of the two divisions is continuous laterally so that externally it is impossible to distinguish the horn from the lower sac, except in so far as the ribs emerge from the horn, and there is a faint groove corresponding with the line along which the two divisions of the left side are apposed. The perforations mentioned above give the dorsal wall of the bladder an alveolate appearance, and indeed they are alveoli (Plate 4, fig. 2). The tissue between the openings is solid and extends medially to the vertebrae, dorsally to the outer wall of the bladder. Each alveolus is lined with *tunica interna*, and there are from six to eight such pits (on both sides or only one, depending on the size of the specimen).

The significance of these differences has yet to be determined. Two possibilities present themselves. One is that the difference is a sexual one (the two large fishes were definitely females, the smaller one probably a male), the other that the swim-bladder changes with growth. If the latter is so, then the condition on the left side in large fishes requires a quite considerable reorganization of tissues, including the delamination of the floor to the dorsal horn so as to form a roof for the lower chamber, and the closing of the alveoli to complete the floor to the horn. I am inclined, in view of these rather complex changes, to favour the idea of there being some sexual dimorphism in swimbladder anatomy ; this point can easily be checked by examining several fishes of known sex.

As mentioned above, the oblique transverse wall provides an almost complete division between the single lumen of the subspherical sac and the divided lumen of the thin-walled abdominal sac. Connection between the three lumina is by means of small, ventrally situated and adjacent apertures contained in a pocket of the wall which I have termed the common vestibule. If the wall is viewed from the front, a small transverse slit is seen in its base lying immediately behind the opening of the pneumatic duct. The dorsal lip of the slit is slightly thickened (Plate 3). This slit forms the entrance to the common vestibule. A small, near circular (U shaped in plan) opening placed at a slight angle to the midline lies just behind the lip ; the walls of the opening are somewhat thickened. This is the entrance to the left

division of the abdominal sac and it lies in the left hand wall of the vestibule. The opening to the right lobe is another small hole with a thickened margin, the thickening being a continuation of that surrounding the other opening. Unlike the opening to the left division, that of the right lies transversely and is in the "posterior" wall of the vestibule; the two openings make an angle of about 100° with one another.

An unusual structure is found on the floor of the subspherical sac. It is a moderately large, roughly ovoid body (the long axis transverse) arising from a nearly square base just in front of the opening to the pneumatic duct (Text-fig. 1). From its position relative to this duct, it could perhaps be referred to as an "epiglottis". In two specimens, this body is erect and occupies the position shown in Plate 4; in the third fish, however, it lies in a different position, as if collapsed. The head now occludes both the opening to the pneumatic duct and that of the common vestibule (Plate 3).

I have examined some sections of the "epiglottis"; unfortunately, the material is rather poorly preserved but at least some idea of its histological organization can be gained. The thick basal pad is composed of rather irregularly arranged dense collagen fibres, with a few elastic elements. The main body, including the ovoid head section has an inner core of cartilage, surrounded by a thick jacket of collagenous-elastic connective tissue. Next to the cartilage, the collagen fibres are irregularly arranged but the greater part of the jacket is composed of densely packed and concentrically arranged collagen fibres. Elastic fibres also occur but are relatively sparse and are irregularly arranged. The cartilaginous core is eccentric, there being a greater thickness of connective tissue on the right side of the "epiglottis"; that is to say, at the broad end of the ovoid. In this broader zone, the area of looser tissue is considerably wider than the concentrically arranged part. No trace of muscle could be found in the body of the "epiglottis"; a few, scattered fibres appear in the basal pad. Externally, the whole structure is covered by a thin, squamous epithelium.

Thus, it seems fairly certain that if in life the "epiglottis" is movable it is not activated by any intrinsic muscles.

The abdominal sac may now be considered. Externally it is a single structure, but posteriorly it is bilobed. Internally, however, the anterior portion is completely divided by a paramedial and vertical septum (Plate 3). Unlike the subspherical sac, the walls of the abdominal sac are relatively thin and invested by a coat of intrinsic musculature. The muscle fibres are arranged vertically and run from the dorsal midline of the bladder (or nearly so) to the ventral midline of the anterior unpaired portion, or to about half way up the median wall of each lobe in the paired portion. This thin layer of muscle is of uniform depth over the entire abdominal sac. If the abdominal sac is punctured it immediately collapses, whereas the subspherical sac retains its shape, such is the greater rigidity of its walls.

It is not at first obvious that the posterior part of the sac is indeed bilobed since the medial aspects of the lobes are closely applied and joined by strands of weak connective tissue. If, however, a blunt probe is inserted anywhere along the

median sulcus and then gently moved in an antero-posterior direction, the two lobes are easily separated over the hind two-thirds of the sac. The anterior third is not divisible. Dorsally, each of the separate lobes is closely applied to the vertebral column and to the underside of the ribs. Anteriorly (*i.e.* in the region of the unpaired part) the dorsal relationships of the sac are more complicated and were described above (p. 382).

Each posterior lobe is a complete tube, with its own coat of superficial intrinsic muscles. Where the lobes fuse medially, the common wall thus formed gives rise to the median septum dividing the lumen of the unpaired anterior part. This septum is thick and consists of a middle layer of *tunica externa* sandwiched between the *tunica interna* which lines each division. Anteriorly, the septum curves dextrally to fuse with the transverse wall separating the subspherical sac from the abdominal sac slightly to the right of the mid line.

The volume and diameter of the anterior compartment with its posterior lobe are the same on right and left sides. Apart from the common vestibule, which links the openings to the left and right compartments, there is no other intercommunication between the two sides, at least in the abdominal region. Internally the walls of the two compartments differ somewhat. Throughout its length the lumen of the left division (in large fishes) is smooth, whereas in large and small fishes the dorsal wall of the right division is alveolate over its anterior half. In the small specimen, the dorsal wall of the left division is also alveolate (see above, p. 382). The dorsal and lateral walls of each division (in fishes of all sizes) are strengthened by numerous, close-set fibrous ramifications which break the otherwise smooth surface of the wall into many narrow and shallow clefts. These fibrous half-bands become broader and more widely separated over the posterior half of the bladder. Throughout, the *tunica interna* is very thin and there are no signs of heavy vascularization. This aspect, too, requires verification from histological sections and examination of fresh specimens.

The posterior limit of the abdominal cavity is formed, in the midline, by the greatly enlarged first anal pterygiophore. To this bony eminence is attached the median wall of each abdominal lobe. From this point posteriorly there is no median wall of *tunica externa*, the two caudal lobes being separated merely by a thin partition of *tunica interna*.

Comparison with Asian Species

Superficially, the two most obvious differences between the abdominal swim-bladder of *N. afer* and that of the Asian species are the penetration of its wall by the first seven ribs, and the bilobed posterior portion. Internally, the differences are more numerous.

The subspherical sac of *N. afer* is homologous with the similarly named portion in the Asian species; this area will be considered first. In both groups the postero-dorsal part of this chamber is produced backwards to form the two dorsal horns overlying the anterior portion of the other abdominal subdivision, the medially divided abdominal sac. Some variation in the extent of overlap seems to exist amongst the Asian species, it being greatest in *N. notopecterus* (personal observations).

However, even in this species the horns are not as long as in *N. afer*. In no Asian species do the horns surround the proximal portions of the ribs ; indeed, the entire abdominal swimbladder lies ventral to them. Neither is there any direct communication between the dorsal horns and the underlying part of the medially divided abdominal sac, as is the usual condition on the right side in large *N. afer* and on both sides in the smaller fish I examined.

Even greater are the differences in the form of the transverse, oblique wall which, internally, separates the subspherical sac from the divided abdominal sac. In all Asian species this wall (the oblique septum of authors) is developed only on the left side, the right hand chamber of the abdominal sac being in direct and wide communication with the lumen of the subspherical sac. As in *N. afer*, the opening to the left chamber is directed dextrally, but there is no well-defined common vestibule, and no Asian species has an "epiglottis" or any similar structure. In these fishes, the pneumatic duct opens into the left-hand chamber, but in *N. afer* the opening is medial and before the common vestibule which surrounds the openings to the left and right hand compartments. These pronounced morphological differences suggest some correlation with differences in swimbladder function.

Whereas in *N. afer* the lumen of the subspherical sac is undivided (except for the low incursion of the vertebral column), in Asian species it is partially subdivided by a velum developed in the dorsal midline, apparently as a continuation of the median septum dividing the abdominal sac.

The posterior part of the abdominal swimbladder in all Asian species is, apparently, a single tube with a complete dorsoventral partition down the midline. Neither Bridge (1900) nor Dehadrai (1957) has reported a bilobed portion and I have been able to confirm its unity in *N. notoapterus*. Dehadrai (*op. cit.*) illustrates a cross section through the posterior abdominal bladder, showing a common median wall (composed of *tunica externa*) which divides the lumen into two chambers ; it is continuous above and below with the *tunica externa* forming the outer wall of the bladder. By contrast, in *N. afer*, the posterior two-thirds of the abdominal sac is distinctly bilobed. Admittedly the medial faces of the lobes are closely applied to one another but loose connective tissue separates two complete and distinct walls.

The internal face of the abdominal sac is smooth in all Asian species ; the anterior portion is never alveolate as in *N. afer* (see above, p. 382).

(ii) Caudal Section of the Swimbladder (Plate 1)

As in Asian *Notopterus*, the caudal swimbladder consists of two lobes, separated medially by the anal fin supports. In *N. afer*, however, the bladder extends further caudad, reaching to the caudal fin origin.

Immediately after leaving the abdominal cavity, the bladder curves sharply downwards and then rises gently upwards so that its posterior third lies at a level slightly above the abdominal part. Over the anterior half of its posterior extent, the depth of the bladder is not noticeably less than that of the abdominal part. But further back the depth gradually decreases until in the last third it is about a fifth of the depth anteriorly.

Ventral diverticula are given off throughout the length of the caudal bladder, there being between 115 and 120 from each lobe in the three specimens examined. Each diverticulum has a relatively broad origin, but soon tapers to a narrow tube. As far as I can determine most diverticula end in a single, fine point, although some may be bifid. The position of the diverticula is such that the deep muscle bundles attached to the anal fin rays lie between and below them. Each diverticulum is covered by the superficial fin muscles and lies above an anal pterygiophore.

Internally, the lumen of each lateral lobe is smooth and roughly D-shaped in section, the convex wall facing laterally. Since the *tunica externa* of the medial walls of the abdominal bilobed bladder ceases at the enlarged first anal pterygiophore, the caudal continuations of these lobes have only thin *tunica interna* inner walls. The external tunic is present over the lateral face, but is somewhat thinner than that of the abdominal sac. The entire lateral face of the bladder is covered by a thin sheet of muscle which has both its insertion and its origin on the bladder; small slips invest the ventral diverticula. This intrinsic swimbladder musculature is thickest anteriorly; over the posterior part of the bladder it is reduced to a very thin sheet a few fibres in depth. The fibres of the muscle sheet are vertically disposed throughout its length.

Although there is no *tunica externa* on the medial face of either caudal lobe, the delicate *tunicae internae* of each side are separated medially by a thin but tough and fibrous membrane extending between the anal pterygiophores. Some communication exists between the two lobes. In the posterior half of the bladder there are small vacuities in the interpterygiophore membrane, interradian in position and situated a little below the roof of the lobe. Apparently the *tunica interna* does not cover the hole, but it must be stressed that this observation was made on preserved specimens where the tunic is fragile and easily torn. Similar interconnections occur ventrally and are more numerous. Indeed, except for a short anterior region there is a vacuity near the origin of each diverticulum. The apertures of the dorsal vacuities are larger than those of the ventral series.

From gross dissections of preserved specimens I get the impression that the epithelium lining the caudal lobes is not highly vascularized (c.f. Dehadrai's 1962 observations in *Notopterus chitala*).

Comparison with Asian Species

The major difference between the caudal prolongations in *N. afer* and the Asiatic species is their greater length in the former (see Johnels, 1954). In no Asian species do the lobes extend to the posterior tip of the body. Judging from published descriptions of Asian species, the caudal bladder extends to slightly beyond a vertical through the dorsal fin; in other words, to a point about mid-way between the anus and the caudal fin origin. Because of the greater swimbladder length in *N. afer* there are many more ventral diverticula in this species (115-120 c.f. 14-18 for the Asian species; Dehadrai, 1957). The diverticula are much narrower in *N. afer* and it appears that whereas bifid diverticula are the rule in Asian *Notopterus* this condition is rare in *N. afer*. Presumed connections between the left and right lobes are described for all Asian species where, as in *N. afer*, dorsal and ventral

vacuities occur in the median wall. It seems likely that ventrally the vacuities in *N. afer* are more proximal in position, and that their distribution dorsally is more irregular. Differences also exist in the distribution of the superficial intrinsic musculature. Dehadrai (1957) figures an unspecified specimen (from its shape, *N. chitala*) in which the muscle covers the dorsal and lateral aspects of the abdominal bladder from behind the subspherical sac. Caudally this muscle deepens to cover the lateral aspects of the bladder but not its dorsal part nor the ventral diverticula. It terminates bluntly at a point above the antepenultimate branched diverticulum. In a specimen of *N. notopterus* I have dissected there is no intrinsic muscle cover on the abdominal section, and in the caudal part it fails to cover the dorsolateral as well as the dorsal parts of the wall; its caudal extension is similar to that figured by Dehadrai (*op. cit.*). Bridge (1900) does not mention any intrinsic muscles in *N. borneensis*, but notes that "The dorsal and external walls of each caecum are invested by a strong aponeurotic membrane the outer surface of which receives the insertions of the inner margins of the fibrous septa separating the caudal myotomes".

In *N. afer* the muscle extends much further dorsoventrally throughout the entire length of the bladder; in the bilobed abdominal section it even extends beyond the ventral midline and runs up the lower part of the median bladder wall. Also, a slip from the main muscle body invests the lateral face of each ventral diverticulum.

(iii) *Cranial (Precoelomic) and Interconnecting Parts*
(Plates 1-3 and Text-fig. 1)

When viewed laterally (Plate 2; Text-fig. 1) the external surface of this section is clearly subdivided into three parts. Anteriorly there is an elongate, cylindrical portion (the lateral lobe of the auditory portion) from the somewhat swollen hind margin of which there arises a short, broad and anterodorsally directed process. A deep, narrow groove separates the cylindrical portion from the succeeding divisions which are shaped like a pair of slightly truncated and contiguous hemispheres separated by a deep and narrow groove. These hemispheres connect with the subspherical sac through a short duct of slightly narrower diameter than either the hemispheres or the subspherical sac. Ventrally these subdivisions are less marked. The lateral aspects of the two truncated hemispheres protrude well beyond the level of the auditory part and, but less markedly, beyond the side of the subspherical sac. In the region of the hemispheres the *tunica externa* is inserted along the dorsolateral margin of the vertebral column, thus encompassing the head of the first rib which emerges through the posterior hemisphere. The *tunica externa* of the auditory chamber inserts along the lateral aspect of the skull (prootic and opisthotic ridge, see p. 391) dorsally, and along the posterior vertical margin of the prootic anteriorly, whilst anteroventrally there is a slight union with the hind end of the parasphenoid. The ventral wall of this chamber, however, hangs well below the level of the basioccipital which it encloses.

Internally, the lumen of the double hemispheres reflects the external subdivisions since the two deep external grooves (one between the hemispheres and one between the auditory chamber and the anterior hemisphere) are represented by high ridges of fibrous tissue running from the vertebral insertion of the *tunica externa* to a low and

broad ridge along the midline of the hemispheres (Plate 3). These vertical ridges are deepest ventrolaterally and also broadest because each bifurcates before joining the median ridge. Since the *tunica interna* lies across the upper part of each bifurcation, the base of the ridge is much broader than its upper part.

The auditory chamber can hardly be considered a paired structure even though its lumen is partially divided by the lower otic region of the skull which occupies a considerable part of its volume. Only at the extreme anterior tip of the chamber is the *tunica externa* attached to the base of the skull, thereby forming a small pocket on each side. Elsewhere, its ventral and lateral walls lie away from the skull. Two paired structures arise from each side of the chamber, the inferior and superior intracranial diverticula. The former are anterior prolongations of the *tunica interna* lining the auditory chamber; each enters the skull through a large foramen between the prootic and basioccipital of its side. Each superior diverticulum is a large, and subdivided, vesicle of *tunica interna* which leaves the posterodorsal part of the auditory chamber through a short duct whose origin lies immediately in front of the internal ridge dividing the chamber from the first hemisphere. These intracranial parts of the swimbladder are discussed later (p. 389).

Although the lateral and ventral parts of the auditory chamber consist of soft tunics, the dorsolateral portion is bony, being a deep, ventrally directed channel formed mostly from the basioccipital but partly by a thin ridge of prootic and opisthotic. Within the upper part of this channel lies the auditory fenestra, an extensive elliptical hole bounded by the prootic, opisthotic and basioccipital, and closed by a thin, very flexible membrane. Since the lower boundary of this fenestra is formed from the basioccipital (in this region, rather inflated) its axis is not vertical but slopes mesially at about 5° from the vertical. The thin *tunica interna* of the auditory chamber is closely applied to the skull region encased by the chamber and thus it comes into intimate contact with the fenestral membrane.

From the anterior, pocket-like corner of the chamber on each side of the skull, a broad finger of *tunica interna* passes obliquely through the prootic-basioccipital foramen and then runs forward intracranially (Text-figs. 1 and 2). This is the inferior intracranial diverticulum. It occupies a chamber in the inflated prootic and pterosphenoid, and ends bluntly just anterior to the pterosphenoid-orbitosphenoid union. The right and left diverticula are separated medially by a thin bony partition formed from the parasphenoid, prootic and pterosphenoid. No intercommunications were discovered.

The other paired intracranial diverticula are superior in position and arise on each side from the posterior part of the auditory chamber (see above, p. 387 and Text-figs. 1 and 2). A short duct, closely applied to the posterior face of the skull, leads from the chamber to the vagus foramen; its lateral and posterior walls are of *tunica externa*, but the anterior wall is provided by the skull. The *tunica interna* lining the duct enters the skull through a short, narrow foramen in the exoccipital bone, separated from the vagus foramen only by a thin bony partition. Once within the cranium, this tube of *tunica interna* expands to form a spacious, near ovoid vesicle, whose walls are closely applied to a similarly shaped chamber lying above

the ear and posterior parts of the brain (see section on skull, p. 391). Because of various projections from the walls and roof of this cavity, the lumen of the vesicle is rather irregular. Each vertical semicircular canal passes through the vesicle of its side and the horizontal canals are contained within the bony floor of the capsule. No septum separates the vesicles which are in broad contact mesially. The anterior wall of the cavity housing these vesicles is very thin but bony. It is deeply indented so as to form a broad V whose apex is directed caudally. On each side of the apex is an irregular perforation (sometimes nearly circular, sometimes a notch) situated in the upper part of the wall. The vesicles extend through the aperture of their respective sides and then expand again to form smaller anterior chambers each shaped like a dorsoventrally flattened ovoid. In alcohol-preserved specimens the anterior vesicles are separated by a near-membranous, slightly bony median septum; no trace of this wall can be found in the dried skull.

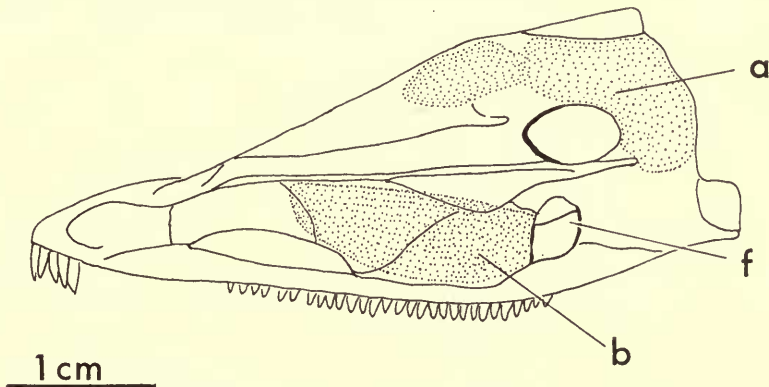


FIG. 2. *Notopterus afer*: lateral view of neurocranium to show position and extent of the intracranial swimbladder diverticula.

a: superior diverticulum; b: inferior diverticulum; f: foramen through which the inferior diverticulum enters the neurocranium.

Some measurements of these intracranial cavities were made from a dry skull; since the *tunica interna* of the swimbladder vesicles is closely applied to the cavity wall, the figures also give some idea of the volume of the vesicles.

Total skull length	. . .	47.0 mm.
Posterior division of the superior cavity (left side)		
Greatest length	. . .	13.0 mm.
Greatest depth	. . .	7.3 mm.
Greatest width	. . .	7.0 mm.
Anterior division of the superior cavity (left side)		
Greatest length	. . .	10.0 mm.
Greatest depth	. . .	4.0 mm.
Greatest width	. . .	6.0 mm.

From the above descriptions it will be seen that in *N. afer* the inner ear is not only in contact with the swimbladder (*via* the lateral auditory chamber and the auditory fenestra) but it is also overlain by diverticula from this organ. Anteriorly

the inferior swimbladder diverticulum wraps around the saccular part of the ear, which is only free from such associations on its medial side where the thin walls of the otic capsules are fused.

Comparison with the Asian Species

It is in the cranial portion that the swimbladders of African and Asian species show the greatest anatomical divergence. No Asian species has any intracranial division of the swimbladder, the auditory chamber is entirely extracranial. In very distinct contrast *N. afer* has not only a somewhat larger extracranial chamber but intracranial diverticula as well, the latter filling the posterior dorsal third of the skull and, at a lower level, extending forward to the orbit. A consequence of these diverticula is a marked difference in the neurocranial architecture of *N. afer* (see p. 392).

The relationship of the swimbladder and the sacculus is identical in both groups but there are differences in the form of the entire auditory chamber. For example, no Asian species shows the two anterior hemispheres which link the auditory and anterior abdominal parts of the bladder in *N. afer*. Instead, there is a very short and narrow portion connecting the subspherical sac with a slightly deeper anterior section which Dehadrai calls the "anterior prolongation of the subspherical sac". Presumably Dehadrai based his observations on *N. chitala* because in a dissection of *N. notopecterus* I find that this prolongation has a much greater depth (almost that of the subspherical sac) than he figures. In fact, its general shape is similar to that of the lateral and ventral auditory chambers in *N. afer*. The illustration of *N. borneensis* given by Bridge (1900) is almost identical with Dehadrai's (1957) figure of *N. chitala*. He describes the anterior prolongation in both species as "Tubular" in contrast to "Rounded, flask-like" for *N. notopecterus* (Dehadrai, *op. cit.*). This part of the bladder is not entirely homologous with the joined hemispheres of *N. afer*, for although it is preabdominal in position it is partly attached to the skull. It seems therefore, to correspond to the posterior, slightly swollen portion of the auditory chamber in *N. afer*. In this species the auditory chamber is not a paired structure, but in Asian species paired processes arise from the "anterior prolongation of the subspherical sac"; these diverge from one another to constitute the anterior, truly auditory portion of the swimbladder. Their homologues in *N. afer* would seem to be those parts of the lateral walls of the auditory chamber overlying the auditory fenestrae. In Asian species the *tunica externa* of the true auditory caecum is inserted onto the skull both dorsally and ventrally so as to form a complete tube. *Notopecterus afer* has the *tunica externa* of the auditory chamber inserted onto the skull only along its anterior and dorsal margins, the ventral part hangs below skull level (forming the ventral auditory chamber) thus making it impossible to consider the auditory portion of the swimbladder as truly paired.

THE SKULL OF *NOTOPECTERUS AFER*

(Text-fig. 3)

Mention was made above of the effects which the intracranial vesicles have on neurocranial architecture. These will be described below in relation to the neuro-

cranium of *N. notopterus* which Ridewood (1904) has described so painstakingly (Text-figs. 3 and 4).

Superficially, the neurocranium of *N. afer* gives an immediate impression of fragility and inflation, particularly in those areas associated with swimbladder diverticula. Since the superior intracranial vesicles are the largest, it is the upper part of the posterior neurocranium that differs most from *N. notopterus*. The periotic region will be considered first. The *opisthotic* is bullate, especially behind. Its ventral face is marked by two deep pits, of which the anterior is deeper and directed posteriorly. In preserved specimens these pits are lined with pockets of *tunica interna* developed from the lateral auditory chamber. Neither pit connects with the superior intracranial vesicle.

The *prootic* is somewhat more bullate than in *N. notopterus*, but the *sphenotic* is much inflated, particularly in the anterior region. By contrast, the *pterotic* is little affected by the general inflation of the otic region. The *epiotic* is greatly inflated so as to become a low cone. In *N. notopterus* this bone is compressed and in transverse section has the shape of an inverted J.

The *exoccipital* shows the greatest inflation of all the skull elements; no aspect is flat and its posterior face (except for a small dorsomedial depression) is strongly convex. In *N. notopterus* there are no convex surfaces and, when viewed dorsally, this bone is V shaped, with the apex facing anteromedially; thus, its posterior aspect is strongly concave. The *foramen magnum* in *N. afer* is depressed and the exoccipitals meet above it in a deep vertical articulation, quite unlike the union in *N. notopterus* which is reduced to a point of contact above the triangular *foramen magnum*.

Other Neurocranial Elements

The *supraoccipital* is slightly broader in *N. afer* and its median crest is greatly reduced. The *parietals* are more domed, as are the *frontals* which meet in a rounded, broad ridge; in *N. notopterus* the frontals meet in a thin, knife-edge ridge. The anteriorly directed frontal ridge which delimits the medial border of the supraorbital sensory channel is much broader in *N. afer*. The direction, depth and arrangement of the sensory canals do not differ markedly in the two species.

The *parasphenoid* differs slightly in that the posterior ascending part (which is preotic in position) is not so definitely a dorsally directed projection as it is in *N. notopterus*; its union with the prootic is along a somewhat dorsally sloping articulation. This part of the bone is inflated so that with the bullate portion of the prootic it forms a noticeable preotic swelling.

The *basioccipital* in the two species is not noticeably different (except that in *N. afer* it shows the papery consistency that so characterizes the skull bones of this fish). However there is no lateral union of the basioccipital and prootic in *N. afer*. Instead, what should be the area of junction is opened out to form the large foramen through which the inferior swimbladder diverticulum enters to the skull. Above this foramen the prootic and basioccipital are joined by a small and rather weak area of contact. The *auditory fenestra* has the same relations in both species; it is perhaps relatively more elongate in *N. afer*.

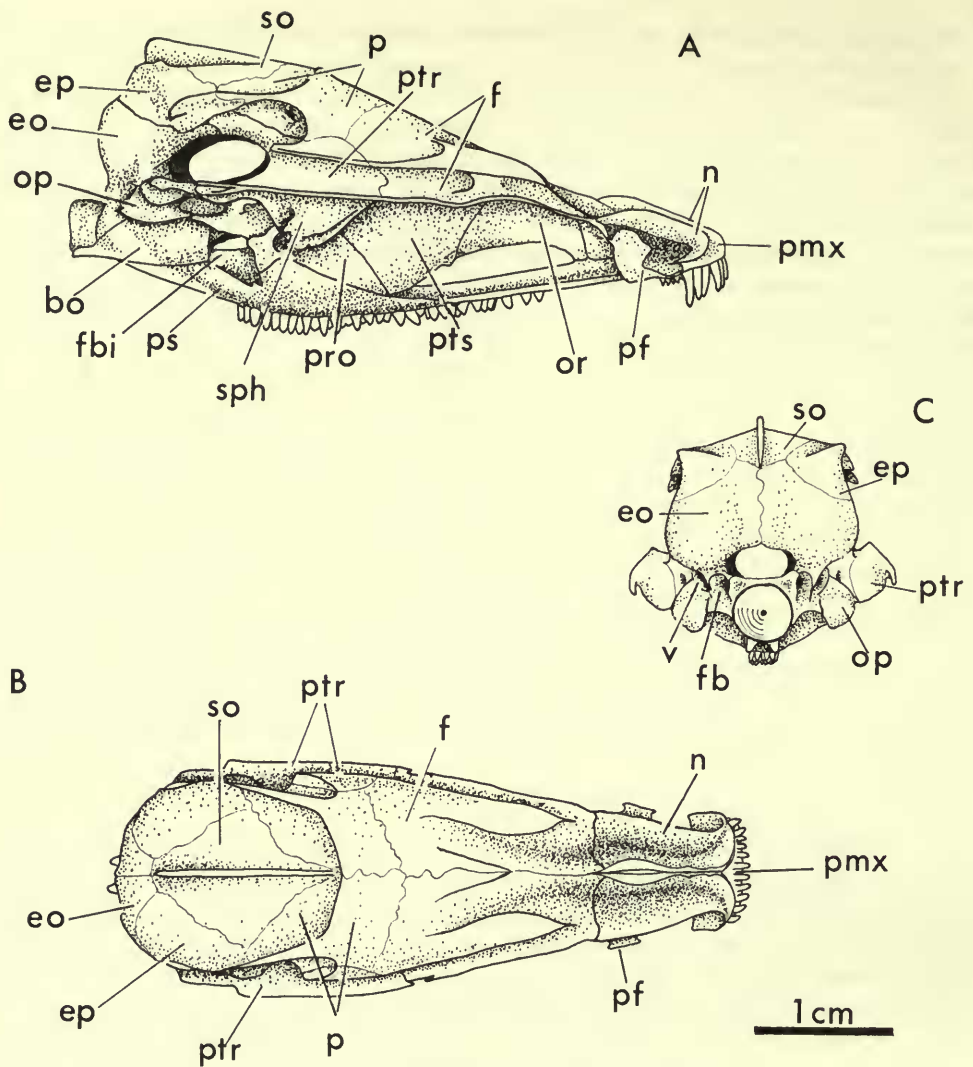
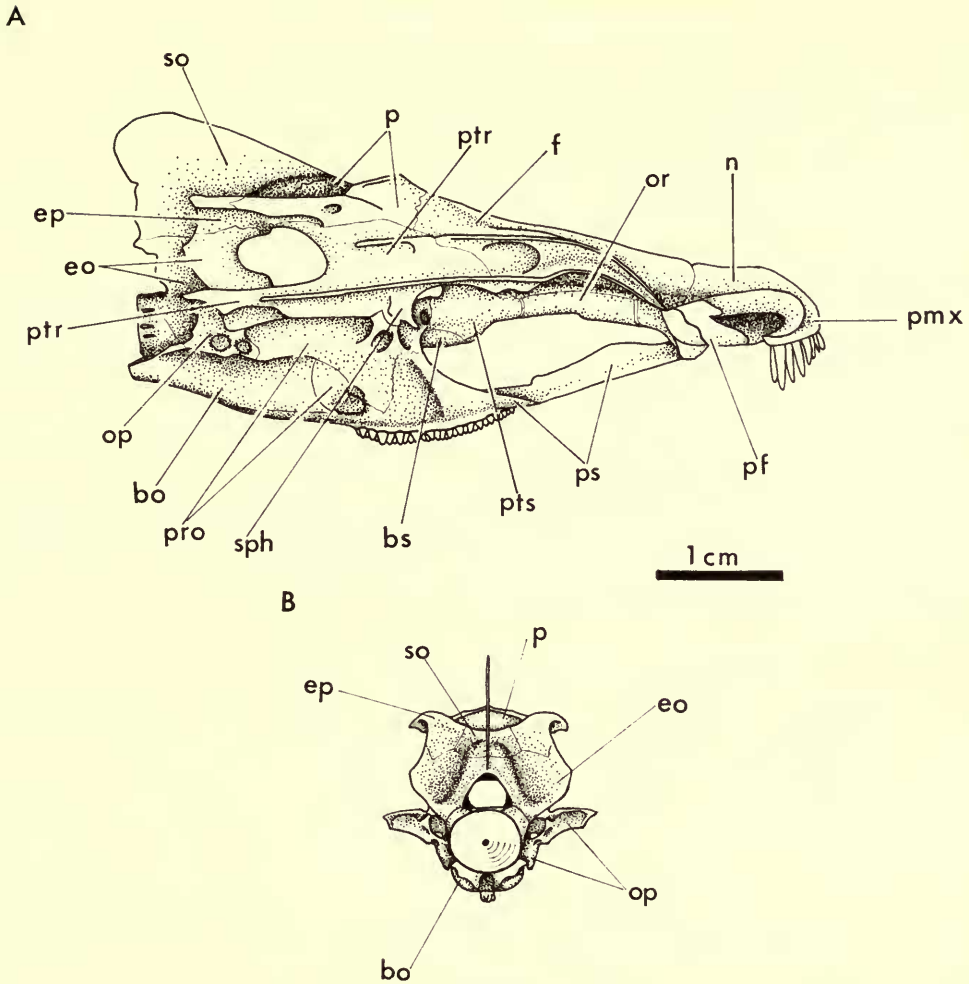


FIG. 3. *Notopterus afer*: neurocranium

A. Lateral view. B. Dorsal view. C. Posterior aspect. bo: basioccipital; eo: exoccipital; ep: epiotic; f: frontal; fb: foramen for swimbladder duct leading to the superior intracranial vesicle; fbi: foramen for inferior intracranial swimbladder diverticulum; n: nasal; op: opisthotic; or: orbitosphenoid; p: parietal; pf: prefrontal; pro: prootic; ps: parasphenoid; ptr: pterotic; pts: pterosphenoid; so: supraoccipital; sph: sphenotic; v: vagus foramen.

The *pterosphenoid* is greatly inflated, both laterally and ventrally, so that its lower, curved margin almost reaches to the level of the parasphenoid; midventrally, the left and right halves barely meet behind the orbitosphenoid. The orbitosphenoid is very bullate; like the pterosphenoid it reaches far ventrally so that the space between these two bones and the parasphenoid is greatly reduced.

FIG. 4. *Notopterus notopterus*

A. Lateral view of neurocranium ; bs : basisphenoid ; all other abbreviations as in Text-fig. 3. B. Posterior aspect.

The *basisphenoid* is very small and is in contact with the parasphenoid. In a small skull I was uncertain whether or not this bone was present.

All the markedly bullate bones, or portions of bone, mentioned above have a characteristically pitted appearance ; in a dried skull many pits are perforated.

The bones forming the anterior part of the neurocranium do not differ greatly in *N. afer* and *N. notopterus*. Likewise, the *circumorbital*, *maxillary*, *mandibular*, *hyo-palatine* and *opercular* series of the two species show no fundamental differences. In *N. afer* only the lower margin of the preoperculum is serrated whereas in *N. notopterus* the lower circumorbitals and the edges of sensory canal gutters in the dentary and upper preoperculum are all strongly serrated.

There is a slight difference in mesopterygoidal dentition. *Notopterus notopterus* has an elongate, narrow patch of enlarged teeth running slightly lateral to the medial margin of the mesopterygoid, and a small patch of minute teeth on the main surface of this bone. *Notopterus afer* has no medial strip of teeth and the minute teeth on the main surface cover almost the entire bone.

Ridewood (1904) noted the presence of a separate opisthotic limb on the *post-temporal* of *N. afer* (absent in *N. notopterus*) but he did not comment on the epiotic limb which is also present, again in contrast to *N. notopterus*.

The *supratemporal* in *N. afer* is larger and less scale-like than in *N. notopterus*; anteriorly it has a moderately large, backwardly directed and wing-like projection. A much smaller, spur-like projection is present near the posterior margin. A short segment of lateral line canal traverses the anterior dorsal angle of the bone; it is continuous with the parietal canal.

The *hyobranchial* skeleton is similar in both species; I count eight branchiostegal rays, but Boulenger found only seven.

Since the skull of *N. borneensis* is like that of *N. notopterus*, apart from its greater lateral compression, it follows that the skull of *N. afer* differs from it in exactly the same characters but with the general inflation relatively more marked. I have been unable to compare the skull of *N. chitala*.

THE SWIMBLADDER OF *XENOMYSTUS NIGRI*

No description of the entire swimbladder in *X. nigri* exists, although Müller (1950) has published a detailed analysis of muscles in the pneumatic duct.

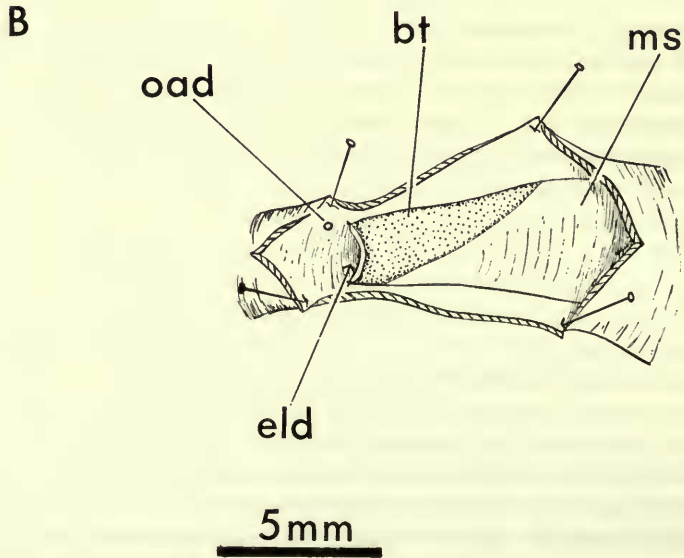
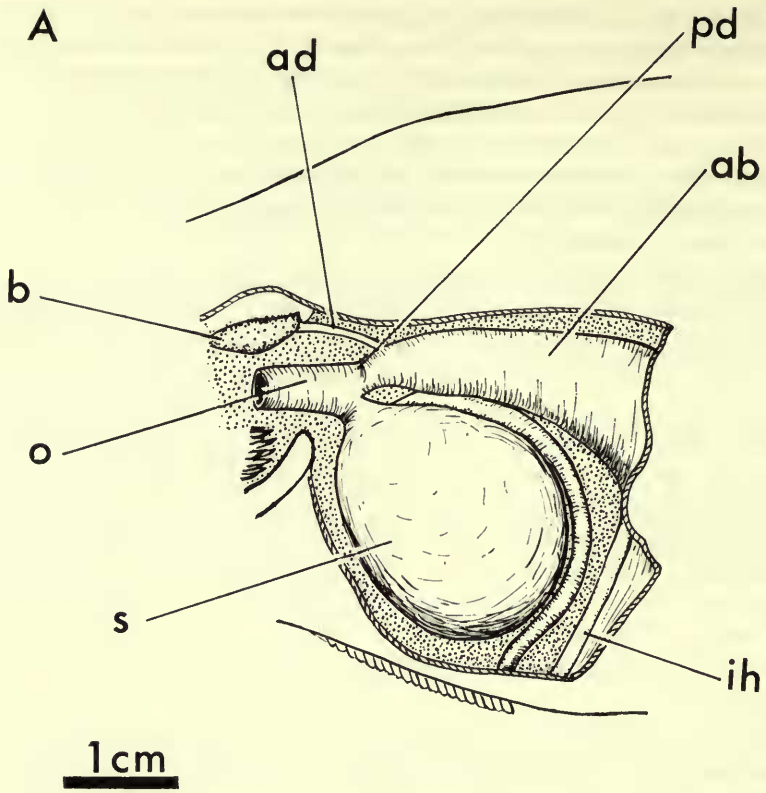
As in *Notopterus*, the swimbladder can be subdivided into cranial, abdominal and caudal parts. The anterior abdominal and the cranial parts are, however, very unlike those of *Notopterus*, as can be seen immediately on dissection (Text-fig. 5A). Whereas in *Notopterus* a large tube runs along the dorsal length of the abdominal cavity, in *Xenomystus nigri* the swimbladder seems to arise from the pneumatic duct as a posteriorly directed tube of moderate proportions. Near the posterior limits of the cavity the tube suddenly deepens so that its lower margin reaches almost to the ventral limit of the abdominal cavity. Throughout its length, the abdominal part of the bladder is a single structure. No anteriorly directed process connecting the cranial and abdominal parts is immediately visible. Further dissection reveals a narrow, slightly curved duct running from the dorsal surface of the main abdominal bladder towards the head (Text-fig. 5A); over most of its course the duct is embedded in kidney tissue. Close to the skull, the duct forks into two very short branches each of which is attached to the skull base. In contrast to the abdominal sac of *Notopterus*, that of *Xenomystus* is very thin-walled. The narrow duct, however, is thick-walled. It will be recalled that in *Notopterus* the anterior abdominal bladder has a much thicker wall than the posterior portion.

The caudal section is strikingly similar to that of *Notopterus* (especially the Asian species) and is provided along its whole length with ventral caeca, strictly interradiar in position and reaching almost to the ventral margin of the body. Few caeca bifurcate distally. There are 70–75 caeca in the four specimens examined. As in

Notopterus, the deep muscles of the anal fin lie between and below the caeca, which are covered laterally by superficial fin muscles. The caudal division extends posteriorly to a point about two-thirds of the length of the post-abdominal body. In a fish 154 mm. S.L., the caudal bladder is 72 mm. long and the post-abdominal body 116 mm. long. The greatest depth is at the anterior end, the depth decreasing regularly thereafter. At the midpoint, the depth is less than half that at its origin; from here posteriorly the depth diminishes rapidly until the last third of the bladder is little more than a narrow tube.

The intrinsic musculature is confined to the caudal bladder where it forms a well-developed sheet running along its entire length. It covers the lateral wall of the bladder except for a narrow dorsal strip extending outwards from the midline; the ventral diverticula are not invested with muscle (c.f. *Notopterus afer* where each is partially covered by a small muscle slip). The muscle fibres are vertically arranged and the entire sheet is supplied by large branches of the eighth spinal nerve. I have dissected four specimens and find that in two the muscle sheet is markedly thicker than in the others where, in fact, it was difficult to distinguish. Unfortunately none of these specimens is well preserved and I could only sex one fish, a male. This has a thin muscle sheet. Perhaps some sexual difference does exist. Size can certainly be eliminated because all four specimens were of approximately the same length. Whether the muscle is relatively thick or relatively thin it is thickest over the anterior three-quarters of its length and becomes very thin near its posterior end.

The cranial part of the swimbladder is short. It consists only of the two anterior forks of the auditory tube, and the paired lateral auditory divisions. Each fork inserts onto a circular rim of bone which surrounds the opening to the auditory chamber of its side. In *Xenomystus* the auditory chamber is of a somewhat different nature from that of *Notopterus* since its walls are entirely bony. *Notopterus* has the lateral and ventral walls formed from the tough *tunica externa*; in the African species there is a common ventral lumen but in the Asian species the chamber of each side is more nearly a separate entity. This process of separation has gone furthest in *Xenomystus* because the lateral and ventral walls of each chamber are replaced by bone (see section on the skull, p. 399). Thus, the chambers are converted to moderately elongate bony blisters situated on the ventral skull surface. Each opens posteriorly by a small, medially directed pore. If the bony lateral wall of a chamber is removed the underlying auditory region of the skull is virtually identical with that of *Notopterus*. That is to say, the lateroventral wall is formed by the slightly swollen basioccipital and, anteriorly, by a contribution from the prootic; dorsally there is a downward facing gutter formed from the prootic (mainly) and opisthotic. Between the upper margin of the basioccipital and the lower, medial margin of the gutter lies an auditory fenestra, closed by a flexible membrane. Relative to the fenestra in *Notopterus*, that of *Xenomystus* is much larger. If the region just described is considered homologous with the lateral auditory chamber in *Notopterus* (particularly the Asian species) then there is also a short intracranial continuation of the swimbladder lodged within the inflated ascending arm of the



parasphenoid. The intracranial projection is subspherical and partially closed off from the auditory chamber by a downward projection of the parasphenoid. As in *Notopterus*, the auditory chamber is lined with *tunica interna* and is thus in close contact with the membrane closing the auditory fenestra.

In essence the swimbladder-auditory linkage in *Xenomystus* is like that of *Notopterus*, except that it is effected through a much narrowed prolongation of the abdominal swimbladder subdivision. The intracranial diverticulum is very slight in comparison with *N. afer*.

The Internal Structure of the Abdominal and Caudal Subdivisions

Little further need be said about the narrow tube connecting the auditory chambers with the main abdominal subdivision. It is of uniform diameter and arises slightly to the right of the midline and a little posterior to the distal opening of the pneumatic duct. The latter is remarkably broad and muscular (see Müller, 1950); its distal opening is marked by a strong sphincter behind which the main abdominal bladder expands slightly and then continues for a short distance before beginning to deepen again. Throughout its abdominal length the swimbladder is a single structure but it is divided internally by a thin, median partition running from just behind the origin of the tubular auditory connection to the enlarged first anal pterygiophore (i.e. the median posterior boundary of the abdominal cavity). The septum extends from the dorsal to the ventral wall of the bladder and is imperforate (Text-fig. 5B). Its anterior margin is thickened and somewhat bowed, the convex surface facing to the left. Immediately behind this lip an elongate and triangular bony plate is embedded in the septum; its anterior edge extends from floor to roof of the bladder and its length is at least half that of the entire median septum (see Text-fig. 5B). The exact nature of the plate and its function have still to be demonstrated. But, from Benl's observations on captive *Xenomystus*, it may be connected with sound production (Benl, 1959).

The lumen of the abdominal bladder is quite smooth and, superficially, shows but slight vascularization.

In all essential details the internal structure of the caudal subdivision is like that of *Notopterus*. I could find no interconnecting vacuities in the dorsal part of the median wall. Ventrally, however, there is a vacuity near the distal end of each caecum except possibly those in the posterior third of the bladder. From preserved specimens it is impossible to determine the extent of superficial vascularization in the caudal subdivision.

FIG. 5. *Xenomystus nigri*

A. Lateral view of abdominal cavity to show the swimbladder and its auditory connection. B. Portion of swimbladder (viewed from left) to show the median septum with the bony triangle embedded therein. The left-hand wall of the bladder has been cut and the edges reflected.

ab : abdominal section of swimbladder ; ad : auditory duct ; b : bony plate covering lateral aspect of auditory chamber ; bt : bony triangle embedded in the median septum ; eld : entrance to right-hand division of the abdominal swimbladder ; ih : first anal pterygiophore ; ms : median septum ; o : oesophagus ; oad : opening of auditory duct ; pd : pneumatic duct ; s : stomach.

THE SWIMBLADDER IN *XENOMYSTUS* AND *NOTOPTERUS* COMPARED

The swimbladder of *Xenomystus* shows a mixture of *Notopterus*-like characters with others unique to the genus. In both genera the caudal portion is basically similar; its shape and size in *Xenomystus* is intermediate between the African and Asian *Notopterus* species. The posterior abdominal portion (i.e. the bladder behind the opening of the pneumatic duct) is nearer the Asiatic *Notopterus* type, but it shows a general simplification of internal structure since its only internal division is a longitudinal one. The bony triangle in the median septum is unique.

It is in the anterior abdominal and cranial subdivisions that *Xenomystus* differs most markedly from *Notopterus*. In the latter genus there is a wide connection between the auditory and abdominal subdivisions whereas in *Xenomystus* the connecting link is reduced to a narrow duct; the auditory chambers are also greatly reduced in volume. In *Xenomystus* the lateral wall of each auditory chamber is a sheet of bone which converts the chamber into a bony, extracranial bulla. The swimbladder-sacculus connection is identical in both genera.

As regards intracranial diverticula, *Xenomystus* shows a slight advance over the Asian *Notopterus* since there is a small inferior diverticulum anterior to the sacculus. This is, however, smaller and much less extensive than the comparable diverticulum in *N. afer* and there is no trace of an upper vesicle.

Although intergeneric differences in swimbladder detail are striking, the overall "bauplan" of this organ in *Xenomystus* is clearly stamped with the notopterid mark.

THE SKULL OF *XENOMYSTUS NIGRI*

Fundamentally, the skull of *X. nigri* is similar to that of the various *Notopterus* species. In certain details it combines characters of both Asian and African *Notopterus*, in others it is unique.

Neurocranium. The outline of the neurocranium differs from that of *Notopterus* in having a convex parasphenoid margin and the otic region rising at a much steeper angle. In this respect it is similar to *Hiodon* (see Ridewood, 1904).

The *etho-vomerine* and nasal regions do not differ from *Notopterus*. The frontals are rather more like those of *N. afer* than the Asian species. The *supraoccipital* is small, its crest reduced and its basal part slopes downwards and backwards unlike the near horizontal position it has in *Notopterus*.

The periotic region. The *prootic* is not markedly bullate except anteroventrally where it meets the ascending parasphenoid limb. I found some difficulty in determining the limits of the *opisthotic*; apparently it has the same proportions and relationships as in *N. afer*. The *sphenotic* is small and not inflated. There is an extensive *pteric*, like that of *Notopterus*, but differing in having the middle section of its supraorbital sensory canal roofed over. The *epiotic* shows some inflation and in this respect is about intermediate between the conditions found in *N. afer* and *N. notopterus*; it has a concave posterior face as in *N. notopterus* but the depression is relatively shallower. The epiotics do not meet above the *foramen magnum* but are separated by a small wedge of supraoccipital. The *basioccipital* is moderately

bullate over most of its length and fairly sharply constricted near its posterior end immediately before the condyle. A ridge runs obliquely forwards and upwards from the posterior tip, passing immediately below the vagus foramen and then becoming continuous with a ridge developed on the ventral face of the opisthotic. In turn, this ridge joins another from the lateral face of the most dorsal part of the prootic. The ridges on the two latter bones face ventrally and are slightly concave. Together with the bones from which it arises, the ridge forms a ventrally directed groove on the side of the skull leading upwards and towards the auditory fenestra. It passes above the fenestra and then curves down around its anterior edge. A similar groove occurs in all *Notopterus* species and is the "ventro-lateral vacuity" of Ridewood (1904). However, unlike *Notopterus*, in *Xenomystus* there is also a flat, horizontal shelf developed along the ventrolateral margin of the basioccipital. This shelf runs onto the bullate floor of the posterior part of the parasphenoid; thereafter it continues vertically upwards as the posterior margin of the ascending parasphenoid limb. The shelf eventually joins the upper ridge (see above). In effect these ridges form a complete wall around the auditory fenestra, situated at some distance from the actual opening. Firmly attached to the rim of this wall is a thin, tear-shaped concavo-convex sheet of bone. Thus on each side a lateral chamber is formed which encloses the otic region of the skull. Anteriorly each chamber ends bluntly within the swollen parts of the parasphenoid and prootic, whilst posteriorly it opens through a small downward and medially facing aperture. This arrangement contrasts strongly with that in *N. afer* where the lateral wall of the auditory chamber is formed from *tunica externa* and right and left sides of the chamber are in direct communication through the common lumen lying below the base of the basioccipital. I consider that the bony lateral cover to the auditory chamber in *Xenomystus* represents an ossification developed in the *tunica externa* of the swimbladder (perhaps during ontogeny?) and that only the margins of the chamber are derived from skull elements. The lower ridge along the basioccipital (not developed in *Notopterus*) may be derived from that bone since no line of union is visible between the ridge and the basioccipital itself. The fact that the bony cover is a single ossification (at least in adults) and that it is separable from the ridge delimiting the auditory chamber seems to argue against its derivation from the same periotic bones that contribute to the ridge. Most of the auditory chamber is extracranial but the anterior portion (that lodged in the prootic and parasphenoid) is truly intracranial. Although both portions are continuous a curved ingrowth from the ascending limb of the parasphenoid subdivides the lumen into unequal anterior and posterior parts, the latter being the larger.

The *auditory fenestra* has the same relationship to the periotic bones as in *Notopterus* but it is relatively larger.

Anteriorly, the *parasphenoid* differs but slightly from that of *Notopterus*, although the part passing through the orbit is narrower and has a distinct ventral curvature. Its teeth are fewer, relatively larger and extend over a greater length of the bone (almost its entire orbital part). Posteriorly there is a well-defined ascending limb (as in *N. notopterus* but not *N. afer*) which is inflated. The posterior ventral part of

the parasphenoid is broad and slightly concave ; it does not extend far beyond the anterior margin of the basisphenoid.

The *orbitosphenoid* and *pterosphenoid* are inflated, especially laterally, and are more like these elements in *N. afer* than those of *N. notoapterus*. Behind the orbitosphenoid the left and right pterosphenoids meet in a fairly extensive union. A small, vertically disposed *basisphenoid* is present. It has a short descending process which meets the ascending arm of the parasphenoid. There is no trace of a posterior myodome.

The *circumorbital*, *opercular*, *maxillary*, *mandibular* and *hyo-palatine* series are of a typical notopterid type. Serrations are present on the margin of the lower circumorbitals, the lower edge of the preoperculum and the margin of its sensory channel, and on the lower margin of the dentary. The interoperculum is greatly reduced and the operculum is relatively smaller than in *Notopterus*.

In the only dry skull available, the *hyobranchial* skeleton is badly damaged but as far as I can see, there are no obvious differences between it and the *Notopterus* type. From dissection I have been able to confirm the presence of paired ventral processes originating near the second basibranchials (a shared notopterid-mormyrid character).

The *posttemporal* is triradiate, with a short epiotic branch and a tubular middle portion ; I cannot find an opisthotic branch.

The *supratemporal* is moderately large and not essentially scale-like. It carries a short length of closed lateral line canal which runs into the parietal canal. In outline this bone is T shaped, with the vertical limb short and the horizontal one deep.

THE TAXONOMIC POSITION OF *NOTOPTERUS AFER* AND *XENOMYSTUS* WITHIN THE FAMILY NOTOPTERIDAE

Günther's original description of *Notopterus afer* deals only with superficial characters. On the basis of these he was certainly justified in separating the one African form as a distinct species. Succeeding authors have followed this arrangement and all have tacitly assumed that *N. afer* did not differ anatomically from its Asian congeners. However, in the light of what is now known about the swimbladder, the relationship of *N. afer* with *N. notoapterus*, *N. chitala* and *N. borneensis* must be reviewed. Dehadrai (1957) has re-examined and compared the swimbladder in the three Asian species. His work shows that some interspecific differences do occur, but compared with the condition found in *N. afer* the Asian species form a relatively uniform group. Above all, none has intracranial swimbladder diverticula, yet extensive intracranial vesicles are a feature of the African *N. afer*. Also, the caudal part of the swimbladder in this species is considerably more extensive and the abdominal section has many unique characters (see p. 380). As might be expected from the intracranial invasion of the swimbladder, the neurocranium in *N. afer* differs considerably from that of any Asian species.

In view of these substantial differences it seems realistic to consider *N. afer* as representing a distinct genus, for which I propose the name :

Papyrocranus gen. nov.

TYPE SPECIES : *Notopterus afer* Günther, 1868.

DIAGNOSIS : A notopterid fish differing from *Notopterus* and *Xenomystus* in the presence of extensive intracranial vesicles from the swimbladder, in the presence of an "epiglottis" at the internal opening of the pneumatic duct, in having an almost complete transverse septum in the abdominal subdivision of the swimbladder, in having the posterior part of the abdominal swimbladder divided longitudinally into two separate lobes, in having the caudal swimbladder subdivision extending to the caudal fin origin, and in having the proximal parts of the anterior six or seven ribs enclosed within the swimbladder.

The name *Papyrocranus* is derived from the Greek *papyrus*, paper-reed and *kranos* a helmet, and refers to the paper-thin roofing bones of the skull. I am indebted to my colleague Dr. Ethelwynn Trewavas for suggesting this most appropriate name.

Since these investigations have also disclosed new details in the anatomy and osteology of *Xenomystus*, its taxonomic status should also be reconsidered.

Xenomystus Günther, 1868

TYPE SPECIES : *Notopterus nigri* Günther, 1868.

Anatomical characters in the swimbladder of *Xenomystus nigri* provide additional grounds for its separation from *Notopterus* and *Papyrocranus* at generic level. However, even in *Xenomystus* no different structures are involved, merely the relative development of various parts which one can consider as common to the basic notopterid plan. But, when the swimbladder anatomy is taken in conjunction with the other generic characters (reduced number of branchiostegal rays and absence of a dorsal fin) then the deviation of *Xenomystus* from *Notopterus* and *Papyrocranus* seems to warrant the separation of the two groups at a higher, probably subfamilial, level.

Thus, the subfamilies of Notopteridae can be defined as follows :—

Notopterinae : Dorsal fin present ; 6–9 branchiostegal rays ; auditory connection with swimbladder wide ; lateral and ventral walls of auditory chamber formed from *tunica externa*. Two genera, *Notopterus* (with three species) widely distributed in south-east Asia ; *Papyrocranus* (monotypic) confined to western Africa.

Xenomystinae : No dorsal fin ; three branchiostegal rays ; auditory connection with the swimbladder through a narrow duct ; auditory chamber completely encapsuled in bone ; median septum of swimbladder with a bony inset. A single genus and species, *Xenomystus nigri* from the Nile, Niger and Congo river systems of Africa.

It is clear that the African notopterids have evolved more extensively than their Asian relatives (even if Fowler's [1941] proposed subgenera are accepted). Despite this continental separation, the genera of Notopterinae have evolved within a fairly definite pattern, and one not fully shared by the Xenomystinae.

SWIMBLADDER FUNCTION IN THE NOTOPTERIDAE

The structure of the swimbladder in the Notopteridae suggests that the organ may

have at least three functions other than its usual hydrostatic one : *viz.*, as a means of aerial respiration, as an accessory auditory organ and, as an instrument of sound production.

Dehadrai's (1962) experimental work on two *Notopterus* species has shown beyond doubt that in these fishes the swimbladder serves as a lung. Johnels (1954) has seen *Papyrocranus afer* gulping at the surface of an overcrowded aquarium, but there are no recorded observations of similar behaviour in nature and no detailed work has been done on the physiology of respiration in this African species. On anatomical and morphological grounds there is no reason to suppose that the swimbladder of *Papyrocranus* should not function like that of *Notopterus*. Unfortunately I was unable to study the vascular organization of the organ, nor could I get adequate histological preparations of the swimbladder epithelium to see if it is as highly vascularized as that of *Notopterus*. In *Notopterus* there are obvious modifications to the vascular system which ensure an adequate blood supply to the organ and a "short-circuited" return of oxygenated blood to the heart (Dehadrai, *op. cit.*). The function of the superficial swimbladder muscles in respiration has not been determined ; Dehadrai suggests that they may serve to expel gas from the bladder, but he was unable to distinguish an inhalent and exhalent cycle in aerial respiratory movements. However, the fish certainly expels bubbles of gas as it swims away from the surface (Dehadrai, *op. cit.*).

Observations on the respiratory habits of *Xenomystus nigri* are also confined to aquarium studies. Müller (1950) and Benl (1959) both record this species as taking air at the surface, an activity I can confirm from observations made in the well-oxygenated tanks at the Aquarium of the Zoological Society of London. Again, there is no physiological evidence that the swimbladder functions as a lung, but its organization certainly suggests such a rôle.

There are definite records of sound production by *Xenomystus nigri*. Benl (*op. cit.*) describes these noises as short, deep, grunt-, belch- or bark-like sounds emitted irregularly and generally as single sounds, rarely in groups of two or three. Some idea of their amplitude may be gathered from the fact that Benl could hear them at distances of six to eight metres from the aquarium. The biological significance of sound production in this species is unknown, but Benl gives evidence that strongly suggests some connection with reproductive activities. Structurally, the complex musculature and shape of the pneumatic duct (see Müller, *op. cit.*) probably have some influence over the quality and nature of the sound produced (see Benl, *op. cit.*). Perhaps the peculiar bony triangle embedded in the median septum of the swimbladder is also involved. It may act after the fashion of the reed in a wood-wind instrument. Doubtless the well-developed superficial swimbladder muscles are also involved in sound production, either to set up vibrations in the contained gas or even to expel the gas through the pneumatic duct.

There are no records of sound production in either *Notopterus* or *Papyrocranus*. Dehadrai (1957) suggests that the vertical hanging septum in the subspherical sac of *Notopterus* could act as a vibrator. No such septum exists in *Papyrocranus*, but the arrangement of openings to the paired abdominal sacs, the epiglottis and the

pneumatic duct suggest a possible means of sound production (if gas is forced through them from the posterior part of the bladder, perhaps by contraction of the superficial muscles). The extensive and much branched caudal bladder may also be involved, acting as a resonator to the superficial muscles as vibrator.

No direct evidence has been obtained to show that the notopterid swimbladder has any role in hearing. The intimate association of swimbladder and auditory fenestrae (the latter in contact with the enlarged sacculus, see p. 388) does, however, suggest that acuity of hearing in the different species may be above that of fishes classed by Dijkgraaf (1960) as "normal". Certainly the ear-swimbladder connection in Notopteridae seems, at least anatomically, to be as intimate and effective as that of the mormyrids and anabantoids, fishes which Dijkgraaf classes with the Ostariophysi as "specialists" in sound reception. Indeed, on anatomical grounds I would place the connection as being nearer the ostariophysine condition than that of the other two specialists mentioned.

THE HIGHER TAXONOMIC POSITION OF THE NOTOPTERIDAE AND THEIR RELATIONSHIP WITH THE HIODONTIDAE AND OSTEOGLOSSIDAE

Classifications of the order Isospondyli published during the past sixty years reflect the uncertainty of our knowledge regarding the interrelationship between the Osteoglossidae, Notopteridae and Hiodontidae, particularly the two latter families. In some schemes there is an implied relationship between the osteoglossids and the notopterids with the hiodontids more distant; in others all three are grouped together. The clearest recognition of close affinity is found in the latest classification of isospondylous fishes (Gosline, 1960, 1961). Here the osteoglossids, notopterids and hiodontids are given superfamily rank and placed in the suborder Osteoglossoidei, itself forming one of the two divisions making the order Clupeiformes.

Gosline does not comment on the degree of relationship existing between the three superfamilies. Other workers (Regan, 1909; Berg, 1947; Norman, 1957) suggest closer affinity between the Hiodontidae and Notopteridae by grouping them in one suborder, and placing the Osteoglossidae in another.

Boulenger (1904) was one of the first authors to give detailed reasons for closely relating the hiodontids and notopterids; he says: "The Fishes which form this family (Notopteridae) may be regarded as an eccentric modification of a type very similar to the preceding (Hiodontidae), with which they agree in most osteological features as well as in the dentition, in the connexion between the air-bladder and the ear, and in the absence of oviducts."

Ridewood (1904), basing his arguments on the swimbladder-ear connection and the cranial osteology, could not accept Boulenger's views. He cautions against the use of the swimbladder connection to imply close relationship, and found several osteological characters which he believed linked the Notopteridae rather more closely with the Mormyridae than with the Hiodontidae. Later, Marshall (1962) repeated Ridewood's view, with particular emphasis on the ear-swimbladder link, and amplified it thus ". But a more significant point is that reliance can only be given to structures that are closely similar in all essential respects". He goes

on to express the view that Ridewood's description of the swimbladder in *Hiodon* suggests that it "is not *closely* like that of a notopterid. In fact the divergence seems substantial".

In order to review these divergent opinions I have dissected the ear-swimbladder connection in two specimens of *Hiodon alosoides*, and reconsidered the osteological evidence. My conclusions are nearer Boulenger's than Ridewood's and Marshall's.

First, evidence from the swimbladder; taken in its entirety, there are few points of resemblance between the notopterid bladder and that of *Hiodon*. The latter has a much simpler structure, lacks internal subdivisions and is confined posteriorly to the abdominal cavity. It is, however, divided into a partly thick-walled precoelomic (*i.e.* auditory) portion and a thin-walled abdominal part. The thick-walled auditory division is in the form of paired vesicles each intimately applied to the otic skull region of its side (dorsally to a ridge on the exoccipital, ventrally to a ridge sloping upwards and forwards along the basioccipital, and anteriorly to the vertical prootic lamina which bisects the auditory fenestra; see Ridewood, 1904). Internally each vesicle is lined with *tunica interna* which, medially, is closely applied to the thin membrane occluding the auditory fenestra. Since the fenestra lies next to the upper part of the sacculus, the swimbladder has, in this respect, the same auditory relationships as in the notopterids. One major difference is in the divided nature of the *Hiodon* auditory fenestra and the associated tunics of the swimbladder. The vesicle of *tunica interna* does not extend forward below the prootic lamina but the *tunica externa* does seem to continue beyond the junction of the thickened, fibrous part with the underlying lamina. The anterior extension of *tunica externa* is thin-walled like the abdominal part of the bladder. It is attached to the prootic around the anterior margin of the auditory fenestra. When pressure is applied to the fibrous vesicle, the thin-walled part bulges outward and forward; I have not been able to discover whether this anterior chamber is filled with fluid or gas. It could well be a lateral extension of the perilymph system.

If only that part of the precoelomic swimbladder lying behind the prootic lamina is considered then the auditory connection in *Hiodon* and the notopterids is "closely similar in all essential respects". But the anterior chamber in *Hiodon* does not find a detailed parallel in any notopterid. The auditory fenestra is delimited by a slightly different arrangement of bones in the two families, but in each case it places the same part of the inner ear in contact with the swimbladder and it is in a comparable part of the otic region (see below). It could be argued that the sum of these characters is not *closely* similar in the two families. But it cannot be denied that they resemble one another in these respects more than either does the Osteoglossidae or any other isospondylous fish. Indeed, if a comparison is made with those members of the Clupei having ear-swimbladder connections one striking point emerges: namely, only in the Hiodontidae and Notopteridae is the connection effected through the lateral wall of the otic capsule. In Clupei an extension of the swimbladder enters the skull and forms one or two vesicles associated intracranially with the sacculus or utriculus. Such intracranial swimbladder diverticula as occur in *Papyrocranus* and *Xenomystus* are certainly not closely similar to the Clupei type.

If one restricts comparison of the hiodontid and notopterid swimbladders to the auditory connection, then the degree of similarity seems to equal that characterizing the group of Clupei which Marshall (1962) isolates as the division Clupeiformes (*i.e.* the families Clupeidae, Chirocentridae and Denticipitidae). Unlike Marshall's Clupeiformes, the Hiodontidae and Notopteridae differ from each other in the way the rest of the swimbladder is organized. *Hiodon* appears to have the more primitive type.

Turning to osteological characters one finds almost general agreement amongst authors that *Hiodon* is more primitive than *Notopterus* (and certainly *Papyrocranus*). However, neither Ridewood (1904) nor Gosline (1960, 1961) believes that the skeleton of *Hiodon* indicates a close relationship with the Notopteridae (see above, p. 403 for Ridewood's comments). The caudal fin skeleton (Gosline, 1960) requires little further comment. It is of a very primitive type and Gosline is unable to derive the notopterid or osteoglossid type from it (or for that matter from the skeletal type found in any living isospondylid). Nevertheless, Gosline grouped *Hiodon* in the Osteoglossoidei because of other characters, principally the low number of caudal fin rays, the nature of its nasal capsule and its type of parasphenoid.

Ridewood (*op. cit.*) made a detailed study of the syncranium and concluded that *Hiodon* had more primitive characters than *Notopterus* and that he could not support Boulenger's views on the relationship of the two genera (see above, p. 403). Three characters most engaged Ridewood's attention—the swimbladder, the lateral cranial foramen with the associated supratemporal, and the paired bones articulated with the second basibranchial in *Notopterus*. I have considered the swimbladder already; the osteological points will be discussed together with others which Ridewood did not consider.

The major neurocranial differences are as follows:— the absence of a lateral cranial foramen in *Hiodon*, the presence in this genus of a clupeid type of auditory fenestra, the membranous outer walls of the cephalic lateral line canals in the Notopteridae compared with the more typical complete bony tubes in *Hiodon*, and the very large canal-bearing supratemporal in that genus compared with the small canal-less bone in *Notopterus*.

In *Hiodon* there is a lateral cranial fenestra (Ridewood's cartilaginous tract), bounded by the parietal, pterotic and epiotic, which Ridewood homologises with the pre-epiotic groove in clupeids. He also suggests homology between the lateral foramen of notopterids (bounded by the pterotic, epiotic and exoccipital) and the pre-epiotic groove. Considering the relative enlargement of the pterotic in notopterids and the fact that the exoccipital has been somewhat displaced by the expanded opisthotic, it seems reasonable to consider the fenestra of *Hiodon* and the foramen of notopterids as homologous structures. The auditory fenestrae in the two families are not very dissimilar when considered as openings into the otic capsule, although the peculiar prootic lamina which divides the fenestra in *Hiodon* is a unique structure. That different bones delimit the aperture in each genus can also be ascribed to the different relative sizes of the otic bones in notopterids. In both these characters *Hiodon* would seem to represent the modern expression of a skull

not far removed from a basic ancestral type which also produced (by differential growth of certain bones, possibly under the influence of the evolving swimbladder) a basic notopterid neurocranium.

The large supratemporal of *Hiodon*, which covers the parietal and a considerable part of the temporal region, certainly differs from the much smaller, scale-like bone of the Notopteridae. It should be noted, however, that the supratemporal of *Papyrocranus afer* is larger than that of *Notopterus* and *Xenomystus*, and that unlike the supratemporal of the former genus it carries part of the transverse parietal lateral line canal. Amongst the isospondyls as a whole the supratemporal shows great variation even within members of a suborder; for example, the differences between *Elops* and *Albula* (Elopoidei) are as great as those between *Hiodon* and *Notopterus*.

Perhaps one should not attach too much importance to the supratemporal as an indicator of phyletic affinity. It is a bone which can be affected by numerous other systems (musculature, relative development of lateral line canals, fenestration of the neurocranium), and in the case of *Hiodon* and *Notopterus* is clearly affected by the marked differences in the cephalic lateral line systems. If anything, the latter might seem to provide a better indicator of phyletic divergence.

In *Hiodon* the cephalic lateral line canals (except the pterotic canal) are enclosed in perforate bony tubes. There is a well-developed parietal branch of the supra-orbital canal but no transverse canal in that bone. Instead, the canal runs through the posterior margin of the supratemporal; the posterior part of the supraorbital canal is also continued onto this bone. The pterotic canal has a bony roof but it is covered only by skin ventrally and laterally except for a short tubular portion posteriorly. Externally, the line of this canal is visible (at least in spirit specimens) as a faint, scaleless groove running immediately above the upper margin of the uppermost circumorbital bone and the operculum respectively. I have not been able to detect whether or not neuromasts are present in the open portion of the canal.

The Notopteridae have a very different system. All the canals, except the parietal transverse canal which is tubular, are deep open grooves, roofed over by skin (see also Omarkhan, 1949); none of these canals opens to the surface. The pterotic, parietal (*i.e.* transverse), preopercular and post-temporal canals have a common junction lateral to the cranial fenestra. This lateral line chamber suggests affinity with the "*recessus lateralis*" of clupeids (Wohlfahrt, 1936) although in notopterids the suborbital canal does not open into it and the membrane sealing off the perilymphatic space is stouter and sometimes covered by a fatty plug. It would be interesting to discover the physiological effects of such close association between the ear and the lateral line. The nasals in the two families also reflect the difference in canal structure; in Notopteridae they are broad gutters whereas in *Hiodon* they are narrow tubes.

Although these differences in the lateral line system are both obvious and trenchant their value as pointers towards phyletic distinctness may not be so great. Indeed, they seem to indicate relationship of a degree comparable with that suggested by the skull and the swimbladder. Already in *Hiodon* there is the beginning of a

notopterid-type of lateral line because the pterotic canal is not completely enclosed by bone and, perhaps of great significance, the lateral line system is in fairly close contact with the ear ; the pterotic canal is separated from the horizontal semi-circular canal by thin bone. Omarkhan (*op. cit.*) drew attention to the correlation between enlarged cephalic lateral line canal systems and an association of this system with the ear. It is difficult to decide from the known examples whether the ear-lateral line connection is established first, or whether the canals enlarge and thus are brought nearer the ear. Be that as it may, *Hiodon* does seem to represent an early stage in the evolution of a notopterid pattern.

The jaw arrangement, especially the anterior articulation of the hyopalatine and maxillary series, is of a primitive type in hiodontids and notopterids. A similar arrangement is otherwise found only in the Osteoglossidae and Denticipitidae. This point is discussed later. The opercular series is complete in the Hiodontidae although the suboperculum is small (absent in Notopteridae) and the interoperculum hidden by the preoperculum, as it is in the Notopteridae. Again, the impression is that *Hiodon* represents an early stage in a trend culminating in the Notopteridae.

In the presence of paired tendon bones attached to the second basibranchial the Notopteridae differ from the Hiodontidae (but, as Ridewood notes, resemble the Mormyridae) ; there is no trace of these bones in *Hiodon*, merely paired tendons.

In both notopterids and hiodontids there are well-developed parapophyses fused to the centra, but the ribs are sessile and articulate with the vertebrae above and well behind the parapophyses. This is an unusual arrangement. In other isospondyls the ribs generally articulate with the parapophyses or, if sessile they lie immediately behind and below the weakly developed parapophyses when these are present.

There are other osteological differences between the two families but they are apparently of little significance from a phyletic viewpoint.

To sum up : the ear-swimbladder connection in the Notopteridae and Hiodontidae is basically similar and is of a kind not found in any other Isospondyli ; the condition found in *Hiodon* could be interpreted as representing an early evolutionary stage in a series leading through *Notopterus* to *Papyrocranus*, with *Xenomystus* as an independent off-shoot. Differences in neurocranial architecture seem explicable on the basis of differential growth in certain elements of the notopterid neurocranium (probably associated with the further evolution of the swimbladder-ear connection) ; again, *Hiodon* provides a basic plan, in this instance linking the notopterid condition with that of the clupeoids. The smaller supratergital of the Notopteridae seems to be associated with the peculiar development of the cephalic lateral line system in that family ; the supratergital is freed from its canal-bearing role by the development of a common lateral chamber from which radiate the canals usually carried by this bone. The cephalic canals of the notopterids are unique ; those of hiodontids suggest a very early stage in the evolution of such a system from a generalized type. The notopterids and hiodontids have a unique arrangement of ribs and parapophyses. Also shared by the two families (and the Osteoglossidae) is the simple anterior arrangement of the hyo-palatine and maxillary bones with the ethmoid region of

the skull. Other osteological differences in the syncrania seem to be of little significance since they occur throughout the Isospondyli and cut across any system of classification. The caudal skeleton of *Hiodon* is a primitive and basic one, that of the Notopterids highly specialized ; however, Gosline is unable to derive the latter directly from the former.

Taking all these characters into consideration, I conclude that the Hiodontidae are more closely related to the Notopteridae than Ridewood (1904) or Marshall (1962) would concede. On the other hand, interfamilial divergence seems sufficiently great to warrant more recognition than that accorded by Berg (1947) or Norman (1957) who separate the two as families within a suborder. Phyletically, it seems correct to place the two groups in one suborder ; perhaps the best indication of their relationship is to give each group superfamily status. In this respect I agree with Gosline (1960), but I do not agree with his action of uniting the Hiodontoidae and Notopteroidae with the superfamily Osteoglossoidae in one suborder (Osteoglossoidei).

The hiodontids, notopterids and osteoglossids are, as Gosline (1960, 1961) has argued, a group readily distinguished from other isospondylous fishes and certainly warranting their segregation into a major division. Diversification within this line has, however, produced three distinctive end-points, two of which are more closely related to each other than either is to the third. This surely indicates that the common stock divided fairly early in its existence, or even its oligophyletic rather than strictly monophyletic origin. Following this reasoning, I believe that the relationships of the three groups are best expressed by uniting the notopteroids and hiodontoids in one suborder and placing the osteoglossoids in another. What status should then be given to the two suborders? Gosline (*op. cit.*) placed them in one Clupeiform division (Osteoglossi) and all other isospondyls in another, the Clupei.

To characterize the division Osteoglossi, Gosline has drawn on the following characters : the possession of a primitive parasphenoid, a parasphenoidal-glossohyal primary bite, the simple arrangement of the hyopalatine-maxillary-ethmoidal articulations (a most distinctive character of the group), peculiarities in the nasal capsule, the parapophyses well-developed and co-ossified with the centra and the low number of principal caudal fin rays ; to these may be added the nature of the swim-bladder-ear connection when this is present. The sum of these various characters sets the division Osteoglossi well apart from the Clupei or any subdivision of the Clupei and it seems reasonable to give the division the formal status of an order (Osteoglossiformes), particularly since this step would emphasize more definitely the phyletic distinctiveness of the group. Gosline apparently did not take the step because he believes that orders and suborders should be interpreted rather broadly and not created for a few aberrant forms (Gosline, 1960). But, although the extant Osteoglossi are few in number, they are hardly aberrant. Rather they appear to be a not particularly successful evolutionary line developed from some pre-clupeoid stem. We know surprisingly little about the ecology of the Osteoglossi and it is thus difficult to suggest why they are an impoverished line. The jaw structure is certainly less flexible (from both the functional and adaptive view-points) than

that of the Clupei and this may have been a restraining factor, as may have been their stenohalinity, for there is only one record of the group in marine deposits.

Judging from their anatomy the Osteoglossi are an ancient group. Since the two suborders are fairly well-defined and both possess unique characters unrepresented amongst living Isospondyli it is difficult to decide which group retains the greater number of "primitive" characters. The Hiodontoidae are, in most respects anatomically less specialized than either the Osteoglossoidae or the Notopteroidae yet the former retain the primitive parasphenoid-pterygoid articulation which is lost in the hiodontoids and notopteroids. Since this articulation may occur as a transient structure in the embryo *Salmo* (de Beer, 1927) its retention in the osteoglossoids may be an adaptive feature. None of the primitive living isodpondyls (*Elops*, *Albula*, etc.) provides a close link with the Osteoglossi. Surprisingly, it is with the recently discovered Denticipitidae (Clausen, 1959; Greenwood, 1960) that I find the most suggestive common characters, although the relationship, if any, is very distant in time as well as morphologically.

The Denticipitidae is a peculiar family of small freshwater and primitive Isospondyli, so far found only in Africa. The living species (*Denticeps clupeoides*, Clausen) occurs in a few localities in Nigeria and the fossil form (*Palaeodenticeps tanganyikae* Greenwood) from a presumed late Tertiary deposit in Tanganyika. Marshall (1962) has suggested a close relationship between *Denticeps* and the Clupeidae, mainly on the nature of the swimbladder-ear connection (which closely resembles that of *Clupea*) and the presence of opercular sensory canals. In other characters too *Denticeps* resembles the clupeids (e.g. the temporal foramen and the auditory fenestra). However, in having a short parasphenoid, simple hypopalatine-maxillary-ethmoidal relationships, enlarged, continuous gutter-like nasals, sessile ribs inserted behind the ankylosed parapophyses, the Denticipitidae shows Osteoglossiform characters. I do not suggest that the living (or recent fossil) denticipitids are close relatives of the Osteoglossiformes (nor for that matter do I support Marshall's close union of the Denticipitidae with the Clupeidae and Chirocentridae). Rather, I suggest that the modern denticipitids are survivors of a formerly more diverse denticipitoid group which, phyletically (and anatomically) speaking, connected the now divergent lines represented by the Osteoglossiformes and Clupeiformes. Much has still to be learned about the modern Denticipitidae and these suggestions are made from a relatively superficial acquaintance with the family. My main reason for disclosing them so prematurely is to bring attention to the family as a potentially important link in our speculations on the phylogeny of primitive Isospondyli.

At present it seems worthless to speculate further on the origin and affinities of the Osteoglossiformes. Nothing discussed above or that I have come across in my researches appears to invalidate the generally held view that the mormyroid fishes were evolved from some branch of the notopteroid-hyodontoid line.

A SYNOPSIS OF THE ORDER OSTEOGLOSSIFORMES

Order Osteoglossiformes

Maxillae without pedicels; palatines end anteriorly in a simple point, without

well-developed maxillary-palatine articular facet (the bones fused in *Pantodon*) ; no supramaxillae ; parasphenoid usually terminating well before the posterior limit of the basioccipital (*Scleropages* is exceptional), generally toothed (*Clupisudis* is exceptional), sometimes with a lateral process for articulating with the endopterygoid (Osteoglossoidei only) ; parapophyses well developed, ankylosed with the centra, ribs either articulating with the parapophyses or sessile ; nasal capsule rigid, without a mobile antorbital-supraorbital pumping device (supraorbital absent or fused with frontal) ; swimbladder-ear connection (if present) not of the clupeid type ; branched caudal fin rays 16 or less.

Two Suborders :

Suborder Osteoglossoidei : parasphenoid process for articulation with endopterygoid ; basisphenoid absent ; nasals enlarged, flattened, suturally united with the frontals and generally with one another (separated medially in *Pantodon*) ; no swimbladder-ear connection ; cephalic lateral line system contained in bony tubes ; ribs articulate with parapophyses.

Suborder Notopteroidei : no parasphenoid process for articulation with endopterygoid ; basisphenoid present ; nasals gutter- or tube-like, sometimes enlarged, sometimes meeting medially, never flattened or suturally united with frontals ; well-developed swimbladder-ear connection ; ribs sessile but parapophyses well developed.

Superfamily Hiodontoidae : separate uroneurals in caudal skeleton ; nasals tubular, separated medially ; cephalic lateral line system contained in bony tubes ; no lateral cranial foramen ; swimbladder not extending posteriorly beyond the abdominal region ; no median septum in swimbladder.

Superfamily Notopteroideae : no separate uroneurals in caudal fin skeleton ; nasals gutter-like, articulating with anterior end of frontals, and meeting one another dorsomedially in the midline (separated in ventral midline by fronto-mesethmoid ridge) ; cephalic lateral line system contained in bony gutters roofed with skin ; well-developed lateral cranial foramen ; swimbladder extending beyond abdominal cavity into caudal region ; median septum developed in swimbladder.

SUMMARY

The swimbladder of *Notopterus afer* is described. It differs considerably from that of the Asian *Notopterus* species, particularly in having voluminous intracranial diverticula and in extending posteriorly to the caudal fin base. The internal organization of the abdominal section is also markedly different, and includes an epiglottis-like structure situated above the entrance of the pneumatic duct.

Because of the intracranial swimbladder vesicles the neurocranium of *N. afer* differs from the type found in Asian species, being more bullate and the bone spongy.

When all these characters are considered it seems advisable to separate *N. afer* as a distinct monotypic genus for which the name *Papyrocranus* is proposed.

The swimbladder and skull of the other African notopterid, *Xenomystus nigri*, are described and compared with *Papyrocranus afer*. In this case the differences warrant the segregation of *X. nigri* in a distinct subfamily (Xenomystinae) ; *P. afer*

and the Asian *Notopterus* species are grouped together as the Notopterinae. Outstanding characters of the *Xenomystus* swimbladder are its narrow connecting duct between the auditory and abdominal parts and the thin bony plate developed in the internal median septum dividing the abdominal part. Only a small paired intracranial diverticulum is present; the auditory diverticula of the swimbladder are encased in bone but are essentially extracranial in position.

The broader taxonomic position of the Notopteridae is considered, particularly in relation to the Osteoglossidae and Hiodontidae. It is concluded that the noto-pterids and hiodontids are fairly closely related to one another and that both are related to the Osteoglossidae. In general these conclusions are in agreement with those of Gosline. However, it is thought that Gosline's division Osteoglossi (of the Clupeiformes) should be raised to ordinal status. Two suborders are recognized, Osteoglossoidei and Notopteroidei, the latter divisible into the superfamilies Hiodontoidae and Notopteroideae (the detailed taxonomy of the Osteoglossoidei is not considered). A possible ancestry for the Osteoglossiformes is discussed.

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